and when consequently

$$a = \frac{R}{v - v_0}, \qquad b = -\frac{\mu}{v^n},$$

we have $e = \mu v^{-n}$,

and

$$I = \gamma - \frac{(n-1)\mu}{v^{n-1}},$$

$$\phi = \Gamma + R \log (v - v_0),$$

$$C - c = \frac{TR^2}{TR + n\mu(v - v_0)^2 v^{-n-1}}.$$

It would be most important if by some method, Kœnig's for instance, or by inserting a small microphone into a tube, the velocity of sound in substances in various states could be accurately determined, as that would enable us to determine C and c separately.

III. "On the Morphology of Birds." By Professor W. K. Parker, F.R.S. Received January 13, 1887.

(Abstract.)

Introductory Remarks.

During the time that the special study of the development of the skull has occupied my attention, the rest of the skeleton has been neglected; it has, however, had its cultivators in no small number.

In a limited degree the skeleton has been worked out by me;—for instance, the shoulder-girdle and sternum in the Vertebrata generally; in birds, the whole skeleton did at one time—a quarter of a century ago—take up much of my thought.

The *development* of the skeleton, generally in this Class, is a subject of great interest, and I am anxious to catch up all the scattered results that lie before me, of the excellent but extremely limited labours of other biologists.

I did begin the study of the development of the limbs, sternum, pelvis, and spine, in 1842, and some of the results will be brought forward in the present paper.

This will be, I trust, but the first-fruits of my most recent work; for, during the long years that have elapsed since this research was fairly begun, I have lost no opportunity of laying up in store embryos and young of birds of many kinds. These stores, if well worked out, will yield a series of papers like the one now offered to the Society.*

* Although I have for many years past kept a register of the presents of

The bibliography of my published papers on the Osteology of the Thorax partly, and of the Skull largely, is given in the general Bibliographical List. It has been necessary to do this, as every scrap and part of the older work is wanted, now that an attempt is made to build the old and the new into something like a structure having form and fulness.

There are several things that go to increase the interest in the morphology of these culminating Sauropsida at the present time.

First.—The discovery by Gegenbaur, Huxley, and others, of the close relationship of birds and reptiles, especially of the extraordinary fact that the hind limb and pelvis of even the most minute bird pass through a stage in which they correspond almost exactly with the hind limb and pelvis of the most gigantic kinds of extinct reptiles—the Dinosaurs or Ornithoscelida.

Secondly.—The recent discoveries of biologists as to the composition of the Cheiropterygium in the various types of air-breathing Vertebrata. It is now well known that the *five-fingered hand* and the *foot with five toes* are the specialised modern representatives of hands and feet that had at least *seven* rays in their composition.

And, *thirdly*—the study of the development and general morphology of birds is, at the present time, of great interest,—now that we are looking to the study of *metamorphosis* for some initial elucidation of the mystery as to the origin of the various types of Vertebrata.

The labour of each succeeding day at this culminating Class makes it more and more impossible for me to conceive of birds as arising *direct* from the Dinosaurians, or indeed from any other order or group of reptiles.

Long attention to the metamorphosis of the Amphibia has intensified this difficulty to me; for the newly-transformed frog or newt appears to me to be the true counterpart of a newly-hatched reptile—snake, lizard, turtle, or crocodile.

Each of these young creatures, whether it has undergone a true metamorphosis, or has been the subject of *pre-natal transformation*, is evidently an *imago;* although an imago that continues to grow.

Now each amphibian has its own *larva*, for the larvæ of the various species have their specific differences.

The thousand known species of existing Amphibia—Anurans, Urodeles, and Cœcilians—and all the fishes that undergo metamorphosis, are as truly, if not as remarkably, distinct from each other in their larval as in their imago form;—as much so as is the case in insects, or any other of those invertebrate types that are truly metamorphic.

materials for this and other parts of my work, I cannot reproduce it here; but must use this opportunity of thanking a host of kind friends for gifts which, in abundance and variety, are somewhat embarrassing.

If *many* of the existing Vertebrata are metamorphic *now*, is it not very probable that they were *all* metamorphic *once?*

The fact that we have, even now, such forms as the larval lamprey (or Ammocœte), the larvæ of Ganoids and Dipnoi, and the tadpoles of newts and frogs, suggests to me the possibility of the existence of huge swarms of low Proto-Vertebrata in the early ages of the inhabited planet.

If such proto-vertebrate forms existed, then it is quite supposable that a metamorphosis may, from time to time, have taken place, of this and that quasi-larval form into archaic reptile, ancestral bird, or primitive mammal.

I am not afraid that anyone familiar with the development, structure, and habits of the existing Amphibia will see any difficulty in the passage of a metamorphic into a *so-called* non-metamorphic type, during time, and under the pressure of new outward conditions, —when the dilemma offered to the supposed low vertebrate was *Transform or perish.*

To me it seems that the creature's necessity was Nature's opportunity; and that, during long ages, the morphological force had accumulated in those low forms an enormous surplusage of unused energy which, in the ripeness of time, blossomed out into this and that new and noble type.

Of all the types of Vertebrata, there is none like the bird of high degree for illustrating what Professor Huxley calls "the threefold law of evolution,"* namely, overgrowth of some parts, starvation and even death of others, and fusion of parts originally distinct.

No kind of vertebrate whatever presents to the osteologist so hopeless an enigma in the adult skeleton as that of the bird; in the overgrowth of certain parts, the abortion or suppresion of others, and the extensive fusion of large tracts of skeletal elements.

Hence this Class has largely acted upon the morphological mind; the "Comparative Anatomist" has, of necessity, undergone evolution into the "Morphologist," and the latter has had to be refined and developed into the "Embryologist."

In the bird class we meet with this remarkable phenomenon, namely, that the swiftest creatures by far that inhabit the earth have had, for the purposes of their most consummate mechanism, the greatest loss of freedom of the individual parts of the skeletal framework.

Between the pigeon, on one hand, above, and the emeu, on the other, below, there are several families of related birds; but there is no direct superposition,—they are *obliquely above or below* each other.

* See his paper "On the Application of the Laws of Evolution to the Arrangement of the Vertebrata, and more especially of the Mammalia" ('Zool. Soc. Proc.,' December 14, 1884, pp. 649–662).

Amongst the Carinatæ, which lie in the intermediate space, there is none better for the purposes of study than the common fowl; to this type I have devoted most attention, and have now worked out the limbs in as many stages as I formerly did the skull.

I can now give an account of the *vertebral column* with *the ribs* and *sternum*, the *limb-girdles* and *limbs*, from the end of the seventh day of incubation; by which time the hyaline cartilage is perfect, and certain even of the bony tracts are begun.

The fowl is an intermediate form between the emeu and the pigeon; but most akin to the latter. I shall now confine myself to what is seen in the development of the skeleton (excluding the skull) in this medium type.

The vertebral column, at the end of a week's incubation, is formed of hyaline cartilage; up to the end of the true sacrals, the notochord is completely invested with cartilage; but, behind those four segments, only at the sides.

The notochord has its constrictions in the middle of each centrum, and is most dilated at the intercentra.

The neural arches do not nearly meet above; the *atlas* is in four pieces—a superficial and an inner piece to the centrum, and a pair of arch-rudiments; the inner segment of the centrum becomes the *odontoid* process of the *axis*.

Between the axis and the first true sacral, all the vertebræ have separate ribs; in the cervical region, except near the dorsal region, there are small styloid cartilages lying horizontally, which have their head, or thick end, wedged in between the upper and lower transverse processes. Near the dorsals they are transversely placed, and then begin to develop a descending process.

The first vertebra of this stage with complete ribs becomes, by absorption of the lower part of the arch, the last cervical in the adult. Behind the twenty pre-sacrals there are fifteen sacrals, and this series has its subdivisions.

The first develops ribs (it is dorso-sacral), the next three develop minute but distinct ribs, like those near the lower part of the neck; these are lumbo-sacral. Then come the four sacrals with no ribs, and then the seven uro-sacrals, the first two of which have rib-bars that ossify separately, below the upper transverse processes, which latter form a complete series from the third cervical to the last free caudal segment.

Of those there are five; then come five more paired imperfect rudiments, clinging to the terminal part of the notochord.

At the end of the 8th day there are *six* of these, with the last elongated, and the notochord projecting behind far enough for three or four more rudiments.

At the end of the 10th day the vertebral chain has undergone a great

change. The *atlas* is still composed of four distinct pieces of cartilages, but the ribs have become fused above and below with the transverse processes, and the notochord is now most constricted at the *intercentra*.

Besides this, in the pre-sacrals, it is constricted in two places within each centrum; so that each centrum in the modern bird corresponds to three subdivisions of this axial chord.

For *two or three days* there is evidence of an archaic subdivision of the notochord into three times as many vertebral divisions as are made now in the modern bird.

In the sacral the constrictions are fewer; they are only at the intercentra, and in the middle of the centrum.

The only absolutely necessary part of the sternum is that where the sternal ribs are attached; that is a very small part, and the rest is for the attachment of the huge muscles that act upon the wings, and for the *obliqui* and *recti abdominis*.

The limb-girdles are each in *three pairs of distinct cartilages*. In front, the scapula, the minute pre-coracoid, the coracoid; behind the ilium, pubis and ischium; the *pre-pubis is part* of the ilium, and that has two regions, the pre-ilium and the post-ilium.

These parts in the bird are not continuous tracts of cartilages, ossified by several centres, but are distinct, first as cartilages, then as bony tracts; those of the *shoulder* keep distinct; those of the *hip* soon coalesce.

The wings at the end of the 7th day are three-toed webbed paws, with all the digits turned inwards. The rods that compose the main part of it are composed of solid cartilage; the humerus, radius, ulna, and 1st and 2nd metacarpals have a bony sheath round their middle part; the ends of the digits and the carpals are but partly chondrified. *Five* carpal nuclei, however, can be made out, and the two proximal nuclei are known to be further subdivided, each into two, in other types; hence we can already account for *seven* carpals in the bird, which has only *two* in the adult, in a free state.

Moreover, the 1st digit has two, and the 2nd three phalanges, the normal number, as in lizards; the 3rd, which should have four, but in birds has as a rule only one, has now two, as in the ostrich, and a few other birds; there is no sign at the end of the 7th or even of the 8th day of incubation of any more than three digits, but we have in the wrist an *intermedio-radiale*, a *centralo-ulnare*, and three distal carpals, answering to the three developed metacarpals. The digits up to the end of the 8th day are rounded and flattish, and are quite like those of a young newt or frog. But in two days more, at the end of the 10th day, the wing has almost acquired the adult form; and one more bony centre, that of the 1st metacarpal, has appeared. The overgrowth of the 2nd distal carpal and the 2nd metacarpal,

with its large and dilated digit, has arrested the distal carpal of the 1st or short digit, the "pollex." This is the last nucleus to chondrify. It is still a very small, limpet-like disk of cartilage, and is now only to be seen on the *flexor face* of the manus, inside the top of the 2nd metacarpal; the distal carpal of the 3rd ray is also small as compared with the large crescentic 2nd distal nucleus. It is thrown on to the ulnar or outer side of the manus, by the overgrowth of the middle rod and its carpal. The curve of the digits at their end is now, not inwards, or to the radial side, but outwards; and the two developed distal segments form now the core of two claws, that of the first, or pollex, being of considerable length.

Thus, by the end of the 10th day, the reptilian type of fore-foot has been attained, and the amphibian type lost; whilst the limb as a whole is now a fore-leg no longer, but a *wing*, thoroughly specialised by evolutional transformation.

The fore-limb has not simply become modified into a wing by the shortening of the pollex and 3rd ray, the enlargement of the 2nd, and the abortion of the 4th and 5th of a fore-paw, like that of the lizard; but we have now the *historical representatives* of three more rays which have cropped up since the end of the 8th day.

I have repeatedly noticed that aborted parts, like overshadowed plants, are late to appear, and soon wither, or are arrested in their growth. This is the case here, for the new rays are late, small, and scarcely functional in the fullest development. They are not lost, however, but, like certain larval structures to be found in the skulls of the highest types of birds, they are built up into the finished wing, although they form an unimportant part of it as far as *function* goes.

The first of these additional rays is the "pre-pollex;" this is a lunate tract of fibro-cartilage attached to the inner face of the 1st metacarpal. The other two are composed of true hyaline cartilage, and appear, one on the ulnar side of the 2nd, and the other on the ulnar side of the 3rd developed metacarpal.

I have described them as *intercalary* metacarpals, for they seem to be the starved twins of the 2nd and 3rd large rays: each distal carpal, very probably, in the archaic forms carried two rays. Thus there is supposed, for such a fore-limb, a digit inside the pollex of the modern bird, and then two pairs of rays, of which only the *inner* in each case has been retained.

The paddle of *Ichthyosaurus* shows this kind of primitive cheiropterygium, admirably.

Thus we can account for seven carpals and six digits in the wing of the modern bird; in the legs the specialisation is not so intense, but is very great; the study of the embryonic stages shows in it many parts that the adult bird gives no signs of whatever.

Instead of there being even two tarsals, free and functional, there is

only one, and that has merely the function of a "sesamoid," and has been mistaken continually for a bone of that sort; that nucleus answers to our *naviculare*, morphologically termed the "centrale."

Notwithstanding the extreme diversity in the habits of existing birds, and the great difference seen in their shank bone, this part is always single, although composed of three metatarsals. As in reptiles, the joint at this part is not between the astragalus and tibia, as in mammals, but through the tarsal series; no sign of this structure is seen in the adult bird. That which appears to be the condyloid end of the tibia is a row of tarsal bones, the tibiale, fibulare, and intermedium; these have long been known as separate bones in young birds, but their distinctness in the early embryo as cartilaginous nuclei has only lately been made out.

I have been able, however, to demonstrate this repeatedly in different kinds of birds. The centrale also, although seen in the embryo as one of the tarsal series, was not properly identified; it is a constant element, but becomes degraded.

The distal series of tarsals exists as a single tract of cartilage, and then as a single plate of bone. But it is related to three metatarsals, and the middle or thick part is the first to chondrify in the embryo, and to ossify in the chicken or young bird; there are here three *connate* nuclei, with very slight signs of distinctness. The whole mass answers to our middle and external "cuneiform bones," and to the inner half of the "os magnum." Thus five tarsals can be always made out clearly, and two more accounted for.

The 1st metatarsal, which has been known, for some time, through the valuable researches of Morse, to have occasionally a proximal as well as a distal rudiment, has, I find, *always* a proximal rudiment as well.

Then, as Dr. G. Baur and Miss A. Johnson have shown, there is a 5th metatarsal; it is a small pisiform cartilage, which soon coalesces with the 4th, and with the great distal tarsal. I can only find a "pre-hallux" by turning to Teratology, and this is not the lawful method.

There may, however, be some "reversion" or "atavism" in the polydactyle foot of the Dorking fowl, which has a well developed "pre-hallux" and a double "hallux;" the twin digits of that part have a very ichthyosaurian appearance.